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# SHORTER ARTICLES AND DISCUSSION

## PIEBALD RATS AND SELECTION, A CORRECTION

In a recent important publication Dr. Sturtevant makes "an analysis of the effects of selection" in which he ably maintains the current view that the single gene is not changed by processes of systematic selection. His argument rests on a careful experimental study of the behavior of the character "dichaet" in *Drosophila,* followed by a general discussion of other work, my own in particular. I am represented as completely opposed to his view, and so I have been at times, but such is not the case at present. I agree so fully with his general conclusion that I want to obviate needless discussion based on the misapprehension.

I thought two years ago that I had evidence that a single gene had changed in the course of a selection experiment, this gene being concerned in producing the hooded pattern of rats. I now find this view rendered untenable by further experiments, the results of which are in course of publication. These results show that the supposed changes in a single gene are more probably due to changed residual heredity, which very likely may consist wholly of other "modifying" genes.

The crucial experiment was one suggested by Dr. Sewall Wright. The divergent hooded races, "plus" and "minus," resulting from selection, were to be crossed repeatedly with a third race, the hooded character being recovered as a recessive in $F_2$ following each cross and its variability compared with that of the uncrossed race. It was believed that if multiple modifying genes were involved, repeated crossing with a pure third race would tend to remove these, in which case the extracted hooded character being deprived of its plus modifiers would be substantially identical with the hooded character deprived of its minus modifiers, as seen respectively in hooded recessives derived from the plus and from the minus crosses. Well, they *are* substantially identical, but it has taken some time and a good deal of trouble to establish the fact. First we had to secure a satisfactory third race to use in the crosses, one free from contamination of any sort by crosses. This we sought in a wild race. But ordinary wild rats will not breed under laboratory conditions. So we resorted to trapping immature wild rats from a single locality and using these as a foundation stock. Crosses with the plus race were then started successfully, but the corresponding experiment with the minus race was hard to get going and so has lagged behind the plus crosses. A report on the result of the plus crosses was made in 1916 (Castle and Wright). The crosses with the minus race were not then sufficiently advanced to show what their outcome would be and this was still true when reply was made to the criticism of MacDowell, as it had been previously when reply was made to Muller and to Pearl, and subsequently when I addressed the Washington Academy of Science on the rôle of selection in evolution (1917). But since then the minus crosses have given what seems to be conclusive evidence that the single gene had not been altered by selection, although the inherited complex responsible for the hooded character had steadily been altered in opposite directions and these alterations were permanent in the sense that they represented racial modes, stable so long as the race was not outcrossed.

I still have on hand a few representatives of the plus and of the minus races which because of their low fecundity it has been impossible to select further for several generations. The two races are very different in appearance. The plus race shows no white except on the under side and sometimes along the flank. The minus race shows no black except a short hood lying anterior to the shoulders, and in an occasional individual a small black spot or two in the middle of the back or on the tail. Yet the variability of each race is still considerable; as measured by our "grades" it has not appreciably diminished in recent generations. The somatic differences entailed by the selection experiments with the hooded character of rats are seemingly greater than those secured by Sturtevant or by MacDowell in regard to bristle number in *Drosophila,* yet I doubt not they may be explained on similar grounds.

Crossing with a wild race affects very differently the plus and the minus selected races. See Tables I and II. The plus race was much less affected than the minus race. Its mean grade was lowered, by three successive crosses with the wild race, not over three quarters of a grade. The standard deviation was about doubled by the first cross. That is the variability of the hooded character, when extracted in $F_2$ from the first wild cross, was about twice as great as the variability of the hooded character in the uncrossed plus selected race. In the second and third crosses the variability declined somewhat, but was still considerably greater than that of the uncrossed race. It was indeed very similar to that of the plus race in the first seven generations of the plus selection experiment. (See Castle and Wright, p. 186.)

TABLE I

RESULTS OF REPEATEDLY CROSSING THE PLUS SELECTED RACE WITH A WILD RACE

| | Mean Grade | Standard Deviation | Number of Hooded Young |
|---|---|---|---|
| Control, uncrossed plus race, generation 10...... | + 3.73 | .36 | 776 |
| *Once* extracted hooded $F_2$ young............... | + 3.17 | .73 | 73 |
| *Twice* extracted hooded $F_2$ young.............. | + 3.34 | .50 | 256 |
| *Thrice* extracted hooded $F_2$ young.............. | + 3.04 | .64 | 19 |

TABLE II

RESULTS OF REPEATEDLY CROSSING THE MINUS SELECTED RACE WITH A WILD RACE

| | Mean Grade | Standard Deviation | Number of Hooded Young |
|---|---|---|---|
| Control, uncrossed minus race, generation 16.... | − 2.63 | .27 | 1,980 |
| *Once* extracted hooded $F_2$ young............... | − .38 | 1.25 | 121 |
| *Twice* extracted hooded $F_2$ young.............. | + 1.01 | .92 | 49 |
| *Thrice* extracted hooded $F_2$ young.............. | + 2.55 | .66 | 104 |

The crosses of the minus race were started six generations later in the course of the selection experiments, with animals of generation 16, minus selection series. They show effects much more striking than those of the plus crosses. See Table II. The minus selected race had now attained a mean of —2.63. A single cross, with the same wild race used in the crosses of the plus series, lower the grade to —.38, extinguishing all the changes in mean grade made by sixteen generations of selection, and leaving the extracted hooded character in a highly variable state (standard deviation 1.25, nearly five times what it had been before). A second cross with the same wild race converted the extracted hooded individuals for the most part into a plus group, mean + 1.01, but with variability somewhat decreased, standard deviation .92. A third cross with the wild race has given extracted hooded individuals *exclusively plus in character,* range from + 1.00 to + 3.50, mean + 2.55. The variability has simultaneously fallen to .66, which is only about one third greater than that of the minus race in the first five generations of the selection experiment. (See Castle and Wright.) One family containing fourteen thrice extracted hooded individuals has a mean grade for the hooded individuals of + 3.05, which is practically identical with the grade of the thrice extracted hooded individuals resulting from the plus crosses (Table I).

It thus appears that three or at most four crosses with a wild race suffice to obliterate all the racial differences which had been induced by ten generations of selection in the case of the plus race and sixteen generations in the case of the minus race. The plus race was changed almost immediately by a single cross, but the change was small (a fact which misled me until the results of the minus crosses were secured). The changes with the minus race were so great that they could not be fully secured by less than three or possibly four successive crosses (eight generations of offspring). The wild race, which we used in our crosses, evidently had a residual heredity much more like that of our plus-selected than like that of our minus-selected race. When the hooded gene from either race was introduced by repeated crosses into this residual heredity, the result was to produce hooded races of very similar grade, a little lower in grade than the plus selected race, but very much higher in grade than the minus selected race.

It thus becomes clear that the changes which had occurred in the hooded character as a result of selection were *detachable* changes and are probably in nature independently inherited modifying factors. This is a view which Phillips and I gave as one of two possible interpretations of the results which we published in 1914. Morgan, Muller, MacDowell and others have insisted that this was the only reasonable interpretation which could be given, but I have not been satisfied with this conclusion in advance of a really crucial experiment, such as I believe has now been performed. Meanwhile the probability that the theory of multiple modifying factors is correct as a general explanation of similar cases has been greatly strengthened by the work of Muller, Bridges, Sturtevant and others, showing that genetic factors, having a definite demonstrable position in linkage systems, influence in a particular way the somatic manifestation of characters varying quantitatively or qualitatively. I accept their interpretations as correct in the light of our present knowledge.

I should feel like apologizing for my own obtuseness in not reaching a similar conclusion sooner, did I not recall with satisfaction how much clearer the rôle of selection now stands revealed than it did when these experiments were begun, and to the clearing up of the situation I shall at least hope that this rat work has contributed something, if only by provoking investigation.

The ''Mutation Theory'' of DeVries gave us a picture of selection as an agency temporarily effective in producing racial changes, but with those changes gradually vanishing as soon as the selection ceased. Johannsen denied within ''pure lines'' even temporary effectiveness of selection. A strictly logical use of Johannsen's conclusions would have limited their application to such organisms as he studied, self-fertilizing ones completely homozygous for all genetic factors and subject apparently to no new changes in such factors. But the doctrine was straightway extended in the views of most geneticists to selection of every sort and he was treated as a traitor to Mendelism who saw any utility in selection or advocated its use as a means of improving the inherited characters of animals or plants.

The situation is wholly different to-day. Through the investigations of Jennings and his pupils on protozoa, of Stout on *Coleus,* and of Shammel on citrous fruits, the fact is clear that even within clones genetic changes may and do frequently occur and that systematic selection will serve to isolate these and thus lead to racial improvement. Those who have tried systematic selection in the case of cross fertilizing organisms have in some cases noted the occurrence of ''mutations'' with such frequency as to make progressive change under selection easily obtainable. Emerson and Hayes, in the case of certain pericarp color patterns of maize, find ''mutations'' so common that a wide range of variability results and selection is able to isolate, from such material, types ''relatively stable,'' but very diverse in appearance. Modifying factors are not involved in Emerson's explanation of his results, but rather such instability of a single gene as leads to frequent mutation. Selection experiments with the variegated coat-patterns of mammals seem to involve less abrupt but otherwise similar changes, but modifying factors rather than repeated mutation seems to be the explanation required in view of the results of crosses reported in this paper.

That selection by one means or another is an effective agency in producing racial changes is not questioned to-day, as it was ten years ago.[1] The only question now at issue is whether the single gene is changeable. I am inclined to think, with Sturtevant, that while single genes do occasionally change producing multiple allelomorphs, a much more common occurrence is change in visible characters through modifying factors. Whether the direction of genetic variation is controllable, other than by the manipulation of modifying genes or the discovery of multiple allelomorphs remains to be determined. The evidence at present is largely negative. It is undeniable that liability to genetic variation is much greater in some organisms than others, much greater as regards some kinds of character than as regards others, but whether we can produce variability of a genetic character is quite a different question. We certainly at present have to follow nature's lead rather than to lead nature, as regards the course of evolutionary change.

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[1] Sturtevant's presentation of my views is a bit unfair in that it seems to imply that whenever I have spoken of "variation in a unit character," I have consistently meant variation in a single gene, whereas in discussing the case of the English rabbit, I have expressly reserved judgment on this point. In a large part of my experimental work, the question under investigation has been—do the visible characters which conform with Mendel's law in transmission suffer modification in crosses or as a result of selection? The present generation of geneticists has apparently forgotten that this was ever a debatable question. We all admit now that contamination occurs in crosses and that modification may be effected by selection, and we seek only to explain *how* the contamination is brought about (as by modifying factors) or *how* the modification is produced in the course of systematic selection (as by the isolation of modifiers in homozygous state). But in the days when the doctrine of gametic purity was under discussion, such "contamination" or "modification" was not admitted.

When Sturtevant denies the occurrence of "contamination," he uses the term in a very restricted sense, not as I have used it in the foregoing sentence, nor as it was formerly used in Mendelian discussions. What he means is not change in the visible character, as the hooded character of rats, but change in a single gene which is known absolutely to limit the manifestation of the hooded character in any form. I agree with his view that there is no conclusive evidence that this single gene had changed in the course of selection experiments, except in the case of our "mutant" race.

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